



The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient enrichment

James E. Cloern

United States Geological Survey, MS496, 345 Middlefield Rd., Menlo Park, CA 94025, USA (Fax: (1) 650-329-4327; E-mail: jecloern@usgs.gov)

Accepted 27 January 1999

Key words: estuaries, eutrophication, resource management

Abstract

Anthropogenic nutrient enrichment of the coastal zone is now a well-established fact. However, there is still uncertainty about the mechanisms through which nutrient enrichment can disrupt biological communities and ecosystem processes in the coastal zone. For example, while some estuaries exhibit classic symptoms of acute eutrophication, including enhanced production of algal biomass, other nutrient-rich estuaries maintain low algal biomass and primary production. This implies that large differences exist among coastal ecosystems in the rates and patterns of nutrient assimilation and cycling. Part of this variability comes from differences among ecosystems in the other resource that can limit algal growth and production – the light energy required for photosynthesis. Complete understanding of the eutrophication process requires consideration of the interacting effects of light and nutrients, including the role of light availability as a regulator of the expression of eutrophication. A simple index of the relative strength of light and nutrient limitation of algal growth can be derived from models that describe growth rate as a function of these resources. This index can then be used as one diagnostic to classify the sensitivity of coastal ecosystems to the harmful effects of eutrophication. Here I illustrate the application of this diagnostic with light and nutrient measurements made in three California estuaries and two Dutch estuaries.

Introduction

Nutrient enrichment of the coastal zone is now a well-established fact. We know, for example, that nutrient loadings to the Baltic Sea, North Sea, Adriatic Sea, Gulf of Mexico, Chesapeake Bay, and San Francisco Bay have increased this century, especially during the rapid growth of population, agriculture and fertilizer production beginning in the 1950's (Nixon, 1995). Coastal eutrophication is a societal concern because anthropogenic nutrient enrichment can stimulate algal production and biomass accumulation, leading to events of anoxia and large-scale mortalities of fish and shellfish (Rosenberg & Loo, 1988).

The study of coastal eutrophication is young and lags by about two decades the effort of limnologists (Nixon, 1995), who produced a set of simple but pow-

erful empirical models of lake eutrophication. These models describe algal biomass as a function of nutrient loading normalized to lake basin morphometry and hydraulics (Dillon & Rigler, 1975; Vollenweider & Kerekes, 1980). They are based on the precepts that phytoplankton biomass (as chlorophyll concentration) is a meaningful indicator of lake trophic status, and that phytoplankton biomass is regulated by the nutrient (P) resource. Our collective study of coastal eutrophication has not yet produced a model analog to describe the functional relation between phytoplankton biomass and nutrient loading, although we have followed the lead of our limnologist colleagues. For example, Gowen et al. (1992) proposed an equation to calculate the potential yield of phytoplankton biomass in coastal ecosystems as a function of nutrient (N) loading. Most reviews of coastal eutrophication

include attempts to find a general empirical relation between algal biomass or production and nutrient concentration or loading (e.g. Boynton et al., 1982; Nixon, 1992; Borum, 1996).

The lake eutrophication models are appealing because of their simplicity, but we are now beginning to suspect that one general loading-plot model of eutrophication might not succeed in the coastal zone. Whereas a clear stimulation of phytoplankton primary production occurred in the Kattegat during the era of nutrient enrichment from the 1950's to the 1980's (Richardson & Heilmann, 1995), other coastal ecosystems such as North San Francisco Bay have experienced declines in phytoplankton production as nutrient enrichment proceeded (Alpine & Cloern, 1992). Chlorophyll concentrations in Chesapeake Bay increased significantly from the 1950s to 1970s when DIN concentrations doubled (Harding, 1994); but chlorophyll concentrations remained unchanged in the Ythan River estuary (Scotland) from the early 1960's to 1990's, when N loading increased fourfold (Balls et al., 1995). Although Delaware Bay and Mobile Bay (USA) have comparable high rates of N and P loading, these estuaries have distinctly different phytoplankton biomass, primary production, and oxygen dynamics (Pennock et al., 1994). Similarly, Vilaine Bay (France) experiences acute symptoms of eutrophication with algal blooms, oxygen depletion, and fish kills (Chapelle et al., 1994), while the nearby Bay of Brest has been resistant to these symptoms even during the past two decades of increased nutrient loading (Le Pape et al., 1996).

In his comparison of algal-nutrient dynamics in 40 estuaries, Monbet (1992) found very different relations between algal biomass and nutrient (N) concentration for tidally energetic and tidally weak systems; he concluded that macrotidal estuaries have an inherent tolerance to nutrient enrichment. Although the evidence is unequivocal that phytoplankton biomass and production are generally related to nutrient loading (Nixon, 1992), there are large deviations around the empirical functions used to describe the algal response to nutrient input (Figure 1a). These deviations imply that we might have great difficulty in finding a simple and robust tool to describe a general eutrophication response in coastal waters, or to classify coastal ecosystems with respect to their susceptibility to eutrophication. Le Pape et al. (1996, p. 1886) suggest that 'Many coastal and estuarine ecosystems are collecting high nutrient loading, but they respond differently to such inputs and it is almost impossible

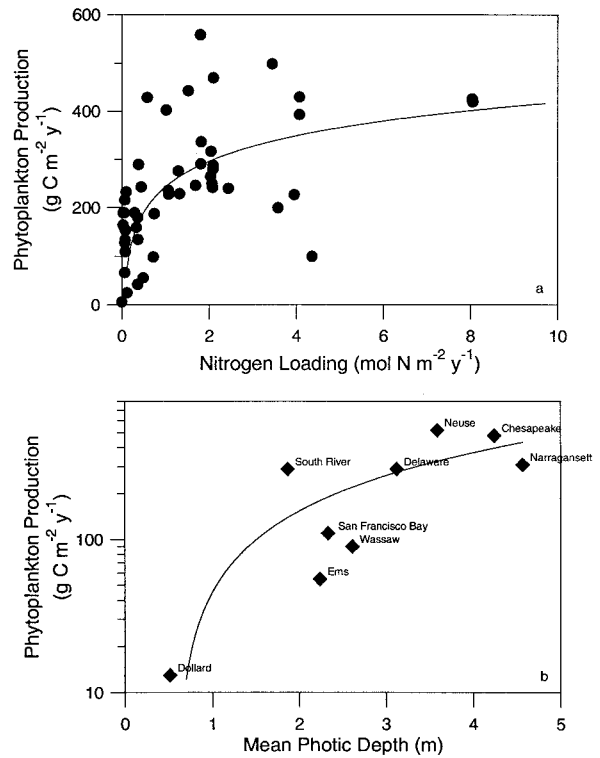


Figure 1. (a) Annual phytoplankton production versus nitrogen loading to shallow coastal ecosystems; from Borum (1996). The fitted curve explains 36% of the variance in production. (b) Annual phytoplankton production in estuaries versus mean photic depth (estimated as the depth of 1% surface irradiance); from Peterson et al. (1987).

to propose a general rule for phytoplankton biomass variability on a seasonal time scale'.

Our failure to find a satisfying analog to the lake eutrophication model is probably a reflection of the extreme diversity of the physical-biogeochemical systems represented by estuaries, tidal rivers, inlets, bays, shelf waters, and river plumes. Among these ecosystems, Visser & Kamp-Nielsen (1996, p. 240) offer the perspective that 'eutrophication is not simply a question of nutrient loading, but (that) the pathways through which nutrients impact on marine productivity are many and varied, being governed as much by physical as biological processes'. As we work to develop general tools to measure the susceptibility of coastal ecosystems to the harmful effects of eutrophication, we need to consider all the physical processes that constrain the phytoplankton response to nutrient enrichment. For example, the transformation of nutrient elements into algal biomass requires solar radiation as the energy source to drive photosynthesis, so the

expression of eutrophication can be constrained by the set of physical processes that govern the availability of sunlight energy to the phytoplankton. This constraint is powerful in turbid coastal systems such as San Francisco Bay (Cloern, 1987), Ems-Dollard estuary (Colijn, 1984), Schelde estuary (Kromkamp & Peene, 1995), and the Mississippi River plume (Lohrenz et al., 1990) where photic zones are shallow, fluctuations in primary productivity are highly correlated with light availability, and where nutrient concentrations are persistently high because the light limitation of photosynthesis also limits the capacity of the phytoplankton to assimilate and transform dissolved nutrients into new algal biomass. Among some coastal ecosystems, light availability appears to be an equally good predictor of phytoplankton primary production as nutrient loading (Figure 1b). Therefore, management strategies to protect coastal ecosystems from acute responses to eutrophication should be developed around the concept that algal population growth and production can be limited by other resources (and processes) in addition to nutrient loading.

Our slowness at developing a general model of phytoplankton resource limitation comes, in part, from the absence of a simple assay for measuring light limitation of phytoplankton in nature. Considerable effort has been directed to assess nutrient limitation with mesocosm experiments (Riemann et al., 1988; Oviatt et al., 1995; Escaravage et al., 1996), bioassays (Granéli, 1987), and measures of algal elemental composition (Paasche & Erga, 1988) or nutrient ratios (Bauerfeind et al., 1990; Fisher et al., 1992). A much smaller effort has been directed to compare light and nutrients as limiting resources, although recent developments have included use of steady-state models of phytoplankton biomass (Carignan & Plenas, 1994), dynamic models of estuarine eutrophication (DeGroot & de Jonge, 1990; Madden & Kemp, 1996), and simple scaling of the light and P resource in lakes against the phytoplankton demands (Millard et al., 1996), as approaches to distinguish conditions of light and nutrient limitation. Pennock & Sharp (1994) combined the light-limitation model of Wofsy (1983) with nutrient bioassays to infer large spatial and seasonal variations in the relative strength of light and nutrient limitation in Delaware Bay. Are there other approaches we can follow to assess the resource limitation of algal growth, and can these approaches be used to classify the susceptibility of coastal ecosystems to the stimulation of algal production in response to eutrophication? Here I suggest one

index of resource limitation, and then illustrate its application with measurements made in estuaries of the Netherlands and California.

A phytoplankton growth-rate model

The analyses presented here begin with a model of phytoplankton population growth:

$$\mu = P^B(\text{Chl:C}) - r, \quad (1)$$

where μ is the specific growth rate (d^{-1}), P^B is daily carbon assimilation rate per unit chlorophyll [$\text{mg C} (\text{mg Chl } a\text{-d})^{-1}$], Chl:C is the ratio of phytoplankton chlorophyll to carbon biomass (g g^{-1}), and r is respiratory loss (d^{-1}). This equation describes algal population growth as the product of the carbon assimilation rate P^B (a function of photosynthetic efficiency and light availability) and the ratio Chl:C (a function of temperature, photo-adaptation, and nutrient availability). Therefore, the model includes functional responses of population growth to both the light and nutrient resources required for the synthesis of new algal biomass. I assume here that the critical nutrient is nitrogen (e.g. Smetacek et al., 1991; de Jonge et al., 1995; Wetsteyn & Kromkamp, 1994; Oviatt et al., 1995), but the analysis can be extended to consideration of limitation by other elements. Other approaches have been used to model algal growth, but the model used here includes an interactive response to light and nutrient availability such that algal growth efficiency in low-light environments is enhanced by nutrient enrichment (Cloern et al., 1995); this interactive effect is not included in models that describe growth rate as the product or minimum of separate light- and nutrient-limitation functions.

Implementation of equation 1 requires functional descriptions of the three components of growth: the photosynthetic rate P^B , the Chl:C ratio, and the respiration rate r . Cloern et al. (1995) fit Equation (1) by least squares to 145 measurements of growth rate and photosynthesis from published experiments with algal cultures, giving estimates of the respiration loss:

$$\mu = 0.85P^B(\text{Chl:C}) - 0.015. \quad (2)$$

The daily carbon assimilation rate P^B can be calculated from the diel- and depth-variations of sunlight, and parameters of the photosynthesis-irradiance function (e.g. Platt et al., 1990):

$$p_{z,t}^B = p_m^B[1 - \exp(-I_{z,t}\alpha/p_m^B)]. \quad (3)$$

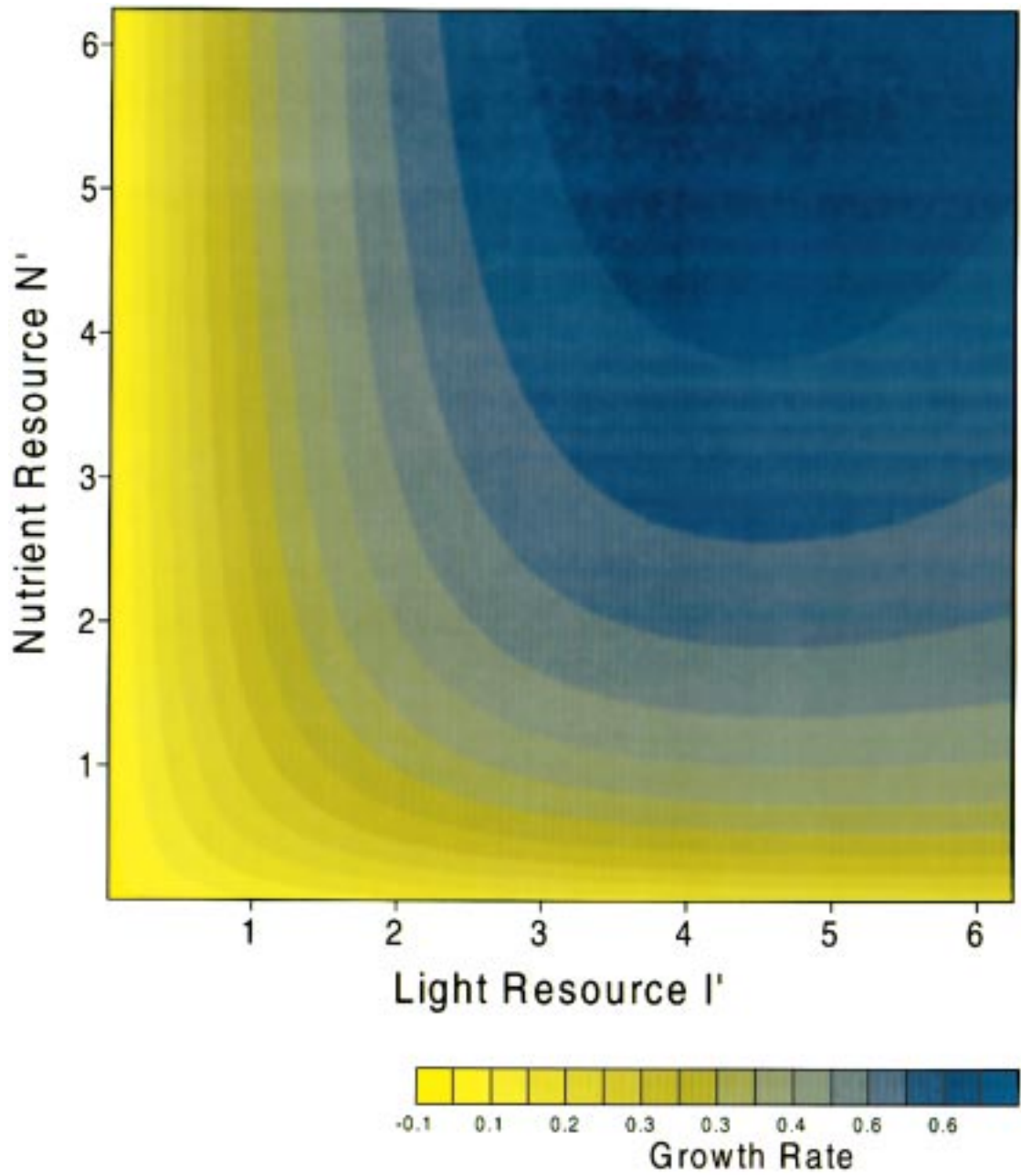


Figure 2. Contours of calculated phytoplankton growth rate (from Equations (2) and (5)) as a function of mean daily light exposure I' ($= I/K_I$) and concentration of limiting nutrient N' ($= N/K_N$). The contours were produced by interpolation (kriging) of growth rates calculated at 7750 combinations of I' and N' between 0 and 6.25 ($= 0\text{--}15 \text{ mol quanta m}^{-2} \text{ d}^{-1}$ and $0\text{--}15 \text{ } \mu\text{M DIN}$, respectively).

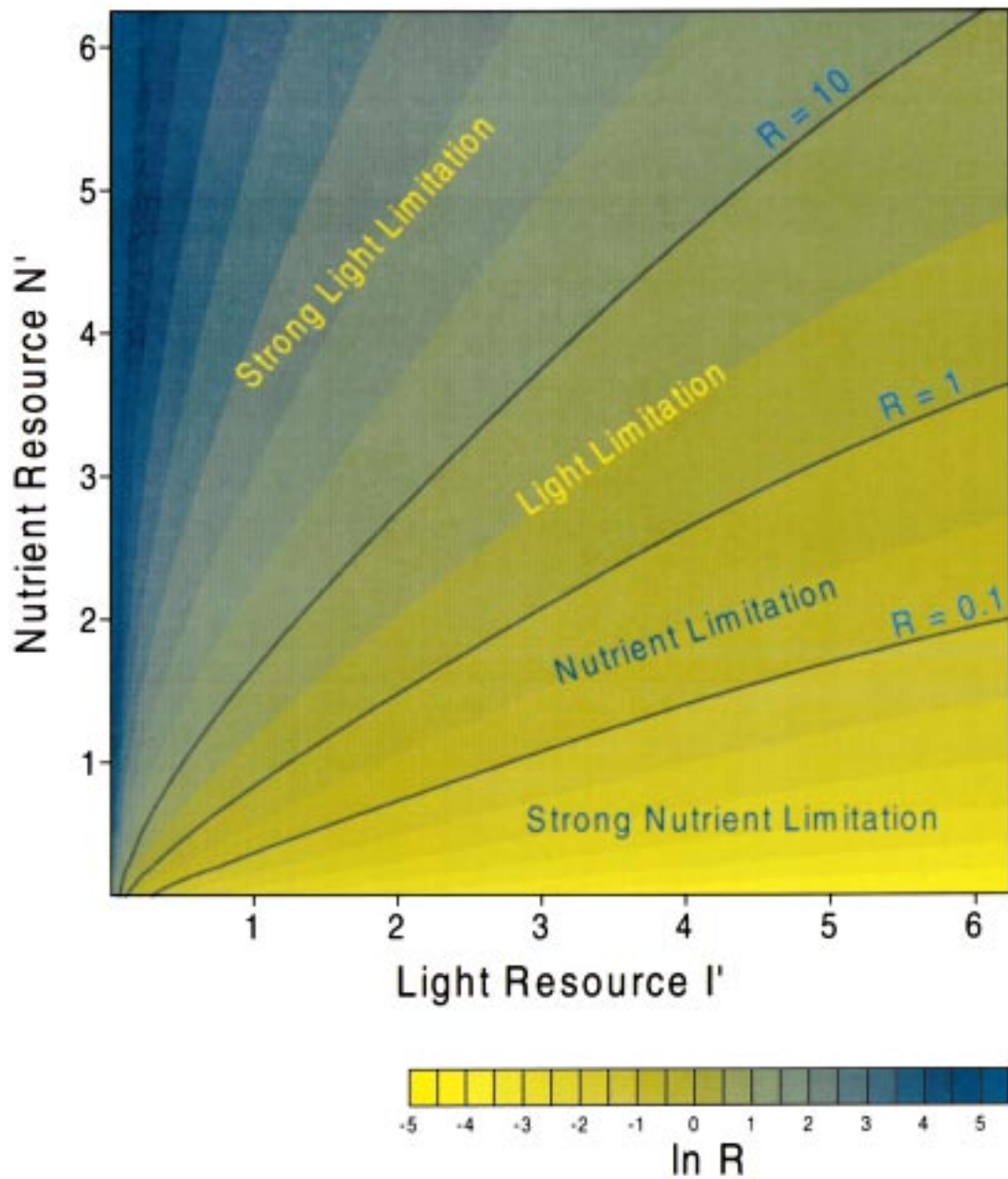


Figure 3. Phytoplankton resource-limitation map as contours of R , the ratio of growth-rate sensitivity to light and nutrients. Large values of R (>10) are resource combinations where growth rate is strongly limited by light availability; small values of R (<0.1) are regions of strong nutrient limitation. The line $R = 1$ defines the combinations of I' and N' for which growth rate is equally limited by light and nutrient resources. This map was produced from interpolation of calculated values of R (Equations (6) and (7)) at 7750 combinations of I' and N' .

Here, $p_{z,t}^B$ is the instantaneous rate of photosynthesis per unit chlorophyll at depth z and time t , $I_{z,t}$ is the instantaneous irradiance (PAR, $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) at depth z , p_m^B the light-saturated assimilation rate, and α defines photosynthetic efficiency at low irradiance. The diel component of light variability can be described as a sin function of photoperiod and irradiance at solar noon (Platt et al., 1990), while the depth variation of irradiance can be described as an exponential decay with the attenuation coefficient k . Then the daily, depth-averaged carbon assimilation rate in a uniform water column (or mixed layer) of thickness H is:

$$\begin{aligned} P^B &= (1/H) \int_0^{24} \int_0^H p_{z,t}^B dz dt \\ &= (1/H) \int_0^{24} \int_0^H p_m^B [1 - \exp(-I_{z,t}\alpha/p_m^B)] dz dt, \end{aligned} \quad (4)$$

Platt et al. (1991) give a series approximation to this integral that can be easily incorporated into a computer program for calculating P^B .

The ratio Chl:C can be estimated with an empirical function fit to published measures of chlorophyll and carbon content of phytoplankton grown under a wide range of light- and nutrient-limiting conditions (Cloern et al., 1995):

$$\text{Chl:C} = 0.003 + 0.0154[\exp(0.050T)] [\exp(-0.059I)][N/(K_N + N)], \quad (5)$$

T is temperature ($^{\circ}\text{C}$), I is mean daily irradiance averaged over depth H [$= (I_\phi/kH)(1 - \exp\{-kH\})$], where I_ϕ is daily surface irradiance as $\text{mol quanta m}^{-2} \text{d}^{-1}$, N is concentration of the limiting nutrient, and K_N is the half-saturation constant for algal growth limited by that element.

Equations (2)–(5) can be used to estimate the growth rate of a phytoplankton population when the following quantities are known or specified: water column height H , daily surface irradiance I_ϕ , light attenuation coefficient k , temperature T , nutrient concentration N , photosynthetic parameters α and p_m^B , and the half-saturation constant K_N . Although each of these quantities influences algal growth rate, the focus here is on the relative importance of light and nutrients as resources that can limit growth. I used Equations (2)–(5) to calculate growth rates across a

matrix of light and nutrient availability, but with fixed values for the other quantities: $H = 10 \text{ m}$; $k = 0.4 \text{ m}^{-1}$; $T = 15^{\circ}\text{C}$; $p_m^B = 7.8 [\text{g C} (\text{g Chl } a-h)^{-1}]$; $\alpha = 0.03 [\text{mg C} (\text{mg Chl } a-h)^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}]$; and $K_N = 1.5 \mu\text{M}$ dissolved inorganic nitrogen, DIN. Equations (2)–(5) were solved for 7750 different combinations of light and nutrient availability, ranging from $I = 0$ to $15 \text{ mol quanta m}^{-2} \text{d}^{-1}$ and N from 0 to $15 \mu\text{M}$. These results define algal growth rate within the light-nutrient space shown in Figure 2, where the two resources have been nondimensionalized for comparison. The light resource I' is daily light exposure I divided by K_I , the daily irradiance at which growth rate is half the maximum ($K_I = 2.4 \text{ mol quanta m}^{-2} \text{d}^{-1}$ when $N = K_N$). The nutrient resource N' is nutrient concentration divided by K_N ($N' = \text{DIN}/K_N$). This figure shows that algal growth rates are small (or negative) near the axes, and they progressively increase away from the origin as light and nutrient resources increase. For this defined set of conditions, the maximum growth rate is about 0.7 d^{-1} , corresponding to a population doubling time of one day.

An index of sensitivity to light and nutrients

Although the specific response of algal growth to light and nutrients depends on all the quantities that influence growth rate, the pattern of responses shown in Figure 2 is general. This general response can be used to estimate the relative sensitivity of algal growth to incremental changes in light energy and nutrient concentration. The shading patterns in Figure 2 depict gradients of the growth rate response to light and nutrients; regions of sharp gradients represent regions of high sensitivity to changing resources. Shading gradients along the x-axis are derivatives of μ with respect to I' ($\partial\mu/\partial I'$), and these measure the sensitivity to light. Gradients along the y-axis are derivatives of μ with respect to N' ($\partial\mu/\partial N'$), and these measure sensitivity to nutrients. The ratio of the two derivatives, $R = (\partial\mu/\partial I')/(\partial\mu/\partial N')$, is an index that tells whether phytoplankton growth rate is more sensitive to changes in light ($R > 1$) or nutrients ($R < 1$).

The growth-rate equation used here cannot be differentiated explicitly, but the partial derivatives $\partial\mu/\partial I'$ and $\partial\mu/\partial N'$ can be evaluated numerically with finite difference approximations. I used the five-point formula (Hildebrand, 1974, p. 111) to calculate:

$$\begin{aligned} \partial\mu_0/\partial I' = & (\mu_{-2} - 8\mu_{-1} + 8\mu_{+1} \\ & - \mu_{+2})/(12hI'), \end{aligned} \quad (6)$$

where $\partial\mu_0/\partial I'$ is the derivative of growth rate with respect to light for a particular combination of I' and N' ; μ_{-1} is the growth rate calculated for the same value of N' but a small ($h = 0.0025$) decrement in I' (i.e., growth rate at irradiance $I' - hI'$); μ_{-2} is the growth rate at irradiance $I' - 2hI'$; μ_{+1} is the growth rate calculated for a small increment in I' (at $I' + hI'$); and μ_{+2} is the growth rate at irradiance $I' + 2hI'$. Similarly, we can evaluate:

$$\begin{aligned} \partial\mu_0/\partial N' = & (\mu_{-2} - 8\mu_{-1} + 8\mu_{+1} \\ & - \mu_{+2})/(12hN'), \end{aligned} \quad (7)$$

where μ_{-1} is now the growth rate calculated for a small ($h = 0.0025$) decrement in the nutrient resource N' , etc.

With this procedure I calculated $\partial\mu_0/\partial I'$, $\partial\mu_0/\partial N'$, and their ratios R at each of the 7750 combinations of I' and N' used to calculate the growth rates in Figure 2. Over this range of I' and N' , the ratio R varies by eight orders of magnitude, so results are displayed in Figure 3 as logarithms of R . The dark shadings in the upper left represent large values of R , regions where the sensitivity of growth rate to light is greater than the sensitivity to nutrients. Lighter shadings toward the lower right are regions of $I'-N'$ space where algal growth is more limited by nutrients than light. These two domains are separated by the middle solid line, where both resources are equally important ($R = 1$). The upper line ($R = 10$) shows the domain where light limitation is ten times stronger than nutrient limitation; the lower line ($R = 0.1$) shows the domain where sensitivity to nutrients is ten times greater than the sensitivity to light.

Results summarized in Figure 3 provide a tool for assessing the relative importance of light energy and nutrients as the two resources that can limit algal growth. We can separate this $I'-N'$ space into five (somewhat arbitrary) domains: strong nutrient limitation, where $R < 0.1$; nutrient limitation ($1 > R > 0.1$); exact colimitation ($R = 1$); light limitation ($10 > R > 1$); and strong light limitation ($R > 10$). From measurements of light I' and nutrient N' availability in an estuary, we can use this resource map to make judgements about the relative strength of light and nutrient limitation at a particular time and location. By examining the distribution of many measurements of I' and N' from one ecosystem,

we can make judgements about the sensitivity of that ecosystem to change in nutrient concentration. For example, if all measured $I'-N'$ pairs from one estuary fall in the domain of strong light limitation, then we can infer that nutrient enrichment will be unlikely to stimulate the growth rate (and biomass) of phytoplankton. Perhaps more importantly from a management perspective, we can also infer from these distributions the magnitude of nutrient reduction that would be required to reduce algal growth rates. The resource map can be used to help develop a management target.

Before implementing Figure 3 as a tool for exploring algal-nutrient dynamics, we should first examine the sensitivity of this resource-limitation map to all the quantities that influence algal growth. In particular, we must determine whether the partition line between the domains of light and nutrient limitation (the line $R = 1$) is fixed, or whether its location is sensitive to changes in the biological (p_m^B , α , K_N) or physical parameters (T) that influence algal growth rate. I did this by recalculating the grid of R values after making incremental changes in the values of T , p_m^B , α , or K_N individually, and then comparing the new locations of the partition line $R = 1$ with the location shown in the reference plot of Figure 3. For example, Figure 4a shows locations of the demarcation line $R = 1$ when growth rates were calculated for $T = 5^\circ\text{C}$ (bottom line) and $T = 25^\circ\text{C}$ (top line), compared to the middle reference location for $T = 15^\circ\text{C}$. Although phytoplankton growth rate varies exponentially with temperature (Equations (2) and (5)), the relative sensitivity of growth rate to incremental changes in light ($\partial\mu/\partial I'$) and nutrients ($\partial\mu/\partial N'$) does not change much with temperature. This suggests that the resource-limitation map of Figure 3 is robust with respect to environmental temperature variability.

Similar calculations were done to compare resource-limitation maps for different values of the half-saturation constant K_N (Figure 4b). This analysis shows that location of the partition line ($R = 1$) is sensitive to the value of K_N chosen to describe nutrient limitation of algal growth rate. This sensitivity grows as irradiance I' increases; at the highest light availability used, the deviation (intercept on the right y-axis) was +30% between calculations done for $K_N = 3\mu\text{M}$ compared to calculations for the reference condition $K_N = 1.5\mu\text{M}$. The partition line deviated -27% from the reference position for calculations done with $K_N = 0.75\mu\text{M}$. The same sensitivity analysis was done to determine shifts of the line $R = 1$ for growth rates calculated with different values of p_m^B (Figure 4c)

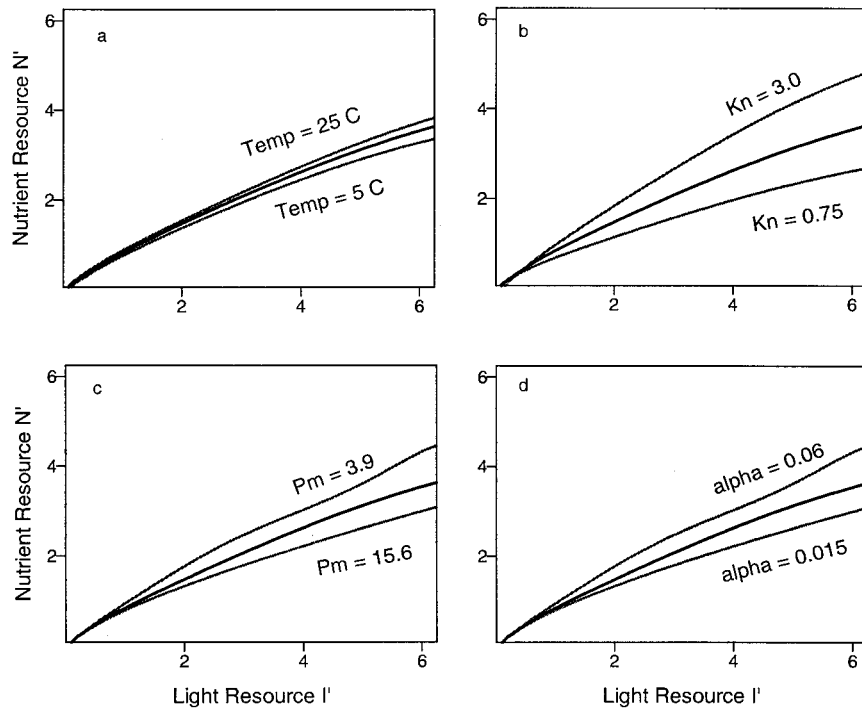


Figure 4. Resource-limitation maps (as in Figure 3) for discrete changes in the model parameters that define phytoplankton growth as a function of light and nutrients. In each case, the solid middle line ($R = 1$) shows the demarcation between domains of light and nutrient limitation for the standard parameter set. Lines above and below show shifts in the location of this demarcation line after incremental increases and decreases in (a) temperature, (b) the half-saturation constant K_N , (c) the maximum assimilation rate p_m^B , and (d) efficiency of photosynthesis at low irradiance α .

and α (Figure 4d). Again, a twofold increase or decrease of these biological parameters caused a shift in the location of the partition line $R = 1$; this shift was most pronounced at high I' . Therefore, the exact partitioning of the resource map into light- and nutrient-limited domains does vary with p_m^B , α , and K_N . However, these deviations are all within the bounds between the lines $R = 10$ and $R = 0.1$ of the resource-limitation map of Figure 3. This sensitivity analysis shows that there is some uncertainty about the exact position of the boundary line between light and nutrient limitation of phytoplankton growth. This boundary shifts with changes in the physiological state of the phytoplankton (p_m^B , α , and K_N), so the domain $0.1 < R < 10$ can be considered a region of potential colimitation by light and nutrients. However, there is no uncertainty about which resource is limiting when measured values of I' and N' fall above the line $R = 10$ (definitive light limitation) or below the line $R = 0.1$ (definitive nutrient limitation).

This sensitivity analysis was designed to encompass the range of physiological and environmental variability expected in temperate estuaries and coastal

waters. For example, in San Francisco Bay water temperature ranges from about 8°C to 24°C ; I' rarely exceeds $10 \text{ mol quanta m}^{-2} \text{ d}^{-1}$ (i.e., $I' < 4.17$); and virtually all measurements of p_m^B and α fall within the ranges ($p_m^B = 3.9 - 15.6$; $\alpha = 0.015 - 0.06$) used here. This range encompasses most of the variability of p_m^B and α measured in other estuaries, such as the Oosterschelde (Wetsteyn & Kromkamp, 1994) and Westerschelde (Kromkamp & Peene, 1995). Most descriptions of nutrient-limited algal growth in the coastal zone specify values of K_N within the range $0.75 - 3.0 \mu\text{M DIN}$ used here (e.g. Chapelle et al., 1994; Prins et al., 1995). Therefore, across the wide range of environments and algal physiological variability expressed within estuarine-coastal ecosystems, the domains of strong nutrient and light limitation shown in Figure 3 appear to be robust criteria for defining the most limiting resource for phytoplankton growth.

Application of the index to measure ecosystem sensitivity to nutrient enrichment

The resource map of Figure 3 provides a simple means of assessing the growth constraints on phytoplankton from measurements of mean irradiance and nutrient concentration. This index can be used to compare the sensitivity of individual estuaries to changes in nutrient concentration. As an example, I apply this index with measurements made in five well-studied estuaries for which the question of resource-limitation has been explored in depth: three estuaries on the Pacific coast of the U.S. (latitude 37° N) and two estuaries on the Dutch North Sea (latitude 52° N).

North San Francisco Bay

The northern reach of San Francisco Bay (California, USA) is the estuary of the Sacramento and San Joaquin Rivers. The upper estuary (Suisun Bay) is highly influenced by river flows that deliver nutrients and sediments. Suspended sediment concentrations in the surface waters are typically in the range 30–100 mg l⁻¹, and the mean light attenuation coefficient in the channel is 4.7 m⁻¹ (Cloern et al., 1985), corresponding to a photic depth of only about one meter. Nutrient concentrations are high: DIN usually > 30 μM, dissolved inorganic phosphorus DIP > 4 μM, and dissolved silicate DSi > 100 μM (Hager, 1994). However, phytoplankton biomass is persistently low, with chlorophyll *a* < 5 μg l⁻¹. This low-chlorophyll high-nutrient condition is the combined result of light limitation of algal growth (Alpine & Cloern, 1988) and rapid grazing by bivalve molluscs (Alpine & Cloern, 1992).

The index of algal resource limitation in North San Francisco Bay is illustrated with light and nutrient measurements made monthly at one location (Figure 5). First, daily irradiance *I* was calculated as $[(I_\phi/kH)(1 - \exp\{-kH\})]$, where I_ϕ is the 3-day mean surface irradiance (mol quanta m⁻² d⁻¹) centered around the sampling date, *k* is the attenuation coefficient, and *H* is water depth at mean tide level. Then, these values were converted to the nondimensional form I' ($= I/K_I$). The nutrient resource was indexed as total DIN concentration (N = the sum of ammonium, nitrate, and nitrite concentrations), and then converted to the nondimensional form N' ($= N/K_N$). With the lone exception in June, all the measurements cluster in the upper left corner of the resource-limitation map (Figure 5), implying

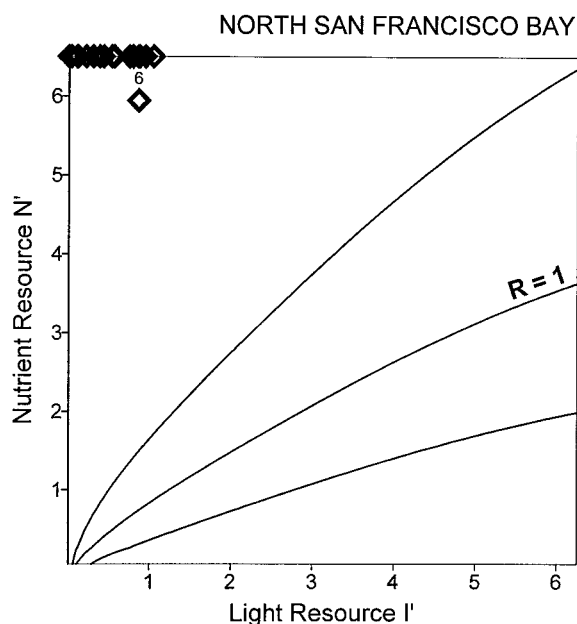


Figure 5. The light and nutrient resources for phytoplankton growth in the upper reach of North San Francisco Bay, from measurements made approximately monthly, January 1992 through November 1993, at a deep station (USGS station 6, Suisun Bay). Diamonds show positions of light and nutrient measurements on the resource limitation map; numbers above indicate the month of sample collection. Daily irradiance (as I') was calculated from the extinction coefficient *k*, mean water depth ($H = 10$ m), and daily surface irradiance. Nutrient concentration N' is the total concentration of dissolved inorganic nitrogen in surface samples, normalized by K_N . Values of N' off the map indicate measurements where $N' > 6.25$ (DIN > 15 μM). Data from Wienke et al. (1993), Hager (1994), and Caffrey et al. (1994).

persistent strong light limitation and small rates of phytoplankton population growth (see Figure 2). This distribution of measurements exemplifies a coastal ecosystem in which high suspended sediment concentration strongly attenuates the light resource and constrains the phytoplankton growth rate. Although highly enriched with N, P, and Si, this estuary does not exhibit symptoms of eutrophication. In fact, annual primary production is only 20 g C m⁻² (Alpine & Cloern, 1992), among the lowest rates of production measured in coastal waters.

South San Francisco Bay

The southern basin of San Francisco Bay is influenced by riverine inputs only during episodes of high discharge, so the suspended sediment concentration (turbidity) is usually lower than in the North Bay and light limitation of algal growth is less severe (Alpine & Cloern, 1988). The South Bay is also enriched

with N and P, but here the nutrient source is dominated by municipal wastewater (Hager & Schemel, 1996). Algal-nutrient dynamics are characterized by autumn-winter periods of low phytoplankton biomass (chlorophyll *a* $\approx 1\text{--}3 \mu\text{g l}^{-1}$) and high nutrient concentrations (DIN $\approx 50\text{--}100 \mu\text{M}$; DIP $\approx 5\text{--}20 \mu\text{M}$; DSi $\approx 80\text{--}160 \mu\text{M}$), followed by a spring phytoplankton bloom when chlorophyll *a* reaches peaks of $50\text{--}70 \mu\text{g l}^{-1}$ and DIN becomes nearly depleted (Cloern, 1996). Light and nutrient measurements from two annual cycles of sampling at one central site (Figure 6) show a more variable distribution of resources than in the North Bay. Here, some observed combinations of I' and N' support high phytoplankton growth rates; nutrient limitation does not occur from summer through winter, but is stronger than light limitation during the bloom peak in March or April, when DIN becomes depleted. As the spring bloom ends and DIN concentrations increase again in summer, the estuary quickly reverts back to the condition of strong light limitation. South San Francisco Bay is an example of a coastal ecosystem in which phytoplankton growth is usually limited by light availability but is episodically limited by nutrients. This implies that further nutrient enrichment might not affect algal growth in summer-autumn, but it could stimulate larger spring blooms than are currently observed.

Tomales Bay

A different combination of growth resources is seen in Tomales Bay, a relatively pristine estuary just north of San Francisco Bay. This estuary has a sparsely populated watershed, smaller nutrient loadings, and lower concentrations of suspended sediments than San Francisco Bay. Measurements from one annual cycle at a central site show that light availability to phytoplankton is always higher in Tomales Bay (Figure 7) than in North San Francisco Bay (Figure 5), but that winter stocks of DIN ($\approx 10\text{--}20 \mu\text{M}$) are much smaller. In winter, light limitation is stronger than nutrient limitation. However as algal biomass increases and DIN becomes depleted in spring and summer, algal growth rates are chronically limited by nitrogen availability. In this estuary, strong nutrient limitation can occur during the months March through August (Figure 7). Tomales Bay exemplifies coastal ecosystems in which phytoplankton growth is frequently limited by nutrients – a situation that implies high sensitivity to changes in nutrient loading.

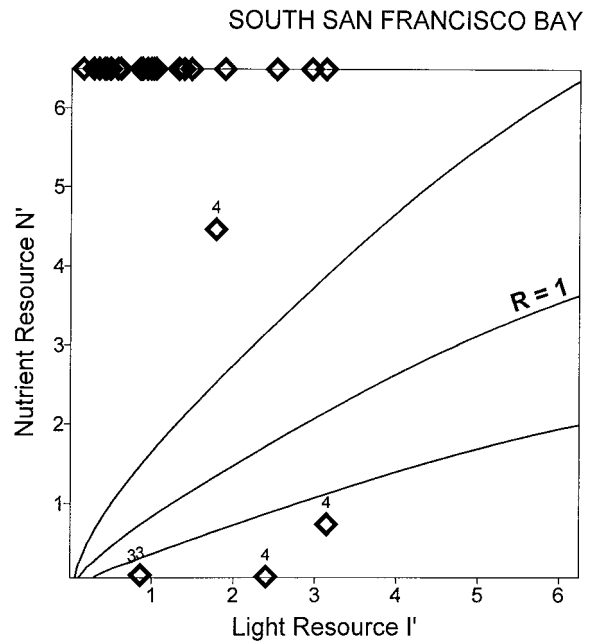


Figure 6. The light and nutrient resources for phytoplankton growth in South San Francisco Bay, from measurements made between January 1992 and November 1993, at a deep station (USGS station 27). Data from Wienke et al. (1993), Hager (1994), and Caffrey et al. (1994).

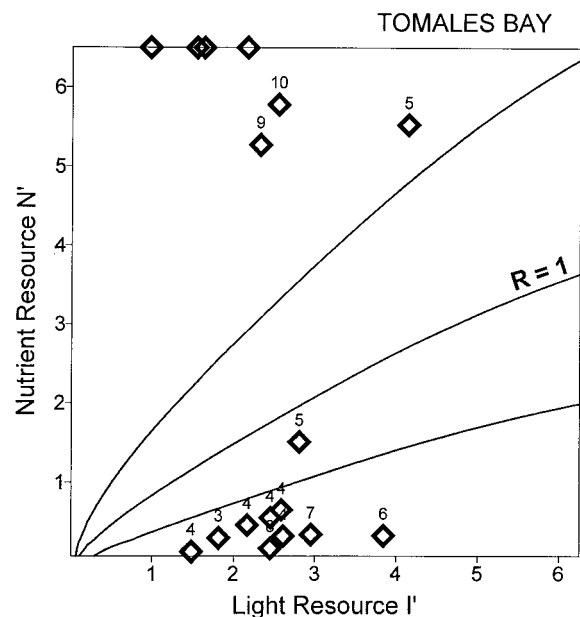


Figure 7. The light and nutrient resources for phytoplankton growth in central Tomales Bay, from monthly measurements between March 1985 and May 1986 (station 8). Data from Cole et al. (1990).

Dutch estuaries

The three cases above show how adjacent coastal ecosystems can exhibit large differences in their sensitivity to nutrient enrichment, depending upon the physical-hydrologic features which regulate light availability to the phytoplankton. Seasonal measurements from two adjacent estuaries in the southern Netherlands exhibit comparable differences in resource limitation. The Westerschelde is highly enriched with N and P, and measurements of light and DIN during 1991 show a pattern of resource limitation (Figure 8) very similar to that in North San Francisco Bay. Although phytoplankton biomass in this estuary fluctuates, with chlorophyll *a* between <1 and $>20 \mu\text{g l}^{-1}$, the DIN concentration is always above $30 \mu\text{M}$ (at Vlissingen, and higher at landward sites (Kromkamp & Peene, 1995)) and light limitation is always stronger than nutrient limitation. The resource index classifies the Westerschelde as a coastal system that is insensitive to fluctuations in nutrient concentration. On the other hand, measurements in the eastern Oosterschelde (Figure 9) show resource distributions similar to Tomales Bay, with light limitation in winter but progressive shift to strong nutrient limitation from May/June through September. Again, two nearby estuaries show very different patterns of resource limitation of algal growth.

A classification of resource limitation

Seasonal distributions of light and nutrient limitation (e.g. Figures 5–9) can be used to compare the potential sensitivity of individual ecosystems to variability of nutrient loading from anthropogenic enrichment or natural processes. One simple index is the frequency distribution of the measurements that show strong light limitation, strong nutrient limitation, or potential co-limitation. Figure 10 is an example, which summarizes these distributions for the five estuaries considered above. North San Francisco Bay and the Westerschelde never exhibit nutrient limitation; these estuaries could be classified as the least sensitive to nutrient variability, and the least susceptible to harmful algal blooms because phytoplankton growth is always constrained by the light resource. South San Francisco Bay is nutrient-limited only about 15% of the time; this estuary does not exhibit acute symptoms of eutrophication now, but the resource index suggests that it might have larger spring blooms in response to further enrichment. The Oosterschelde, and especially Tomales Bay, are often nutrient limited (Figure 10);

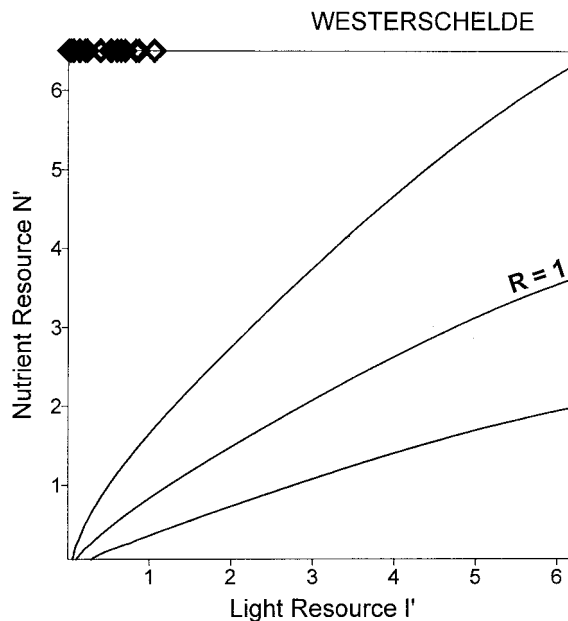


Figure 8. The light and nutrient resources for phytoplankton growth in the Westerschelde, from monthly or semi-monthly measurements at Vlissingen, January through December 1991. Data provided by J. Kromkamp.

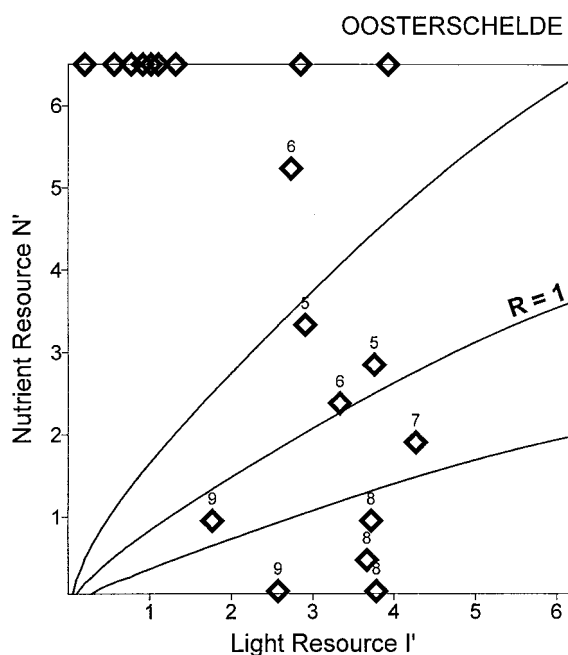


Figure 9. The light and nutrient resources for phytoplankton growth in the eastern Oosterschelde, from monthly or semi-monthly measurements at station LG-PK, January through December 1991. Data provided by J. Kromkamp.

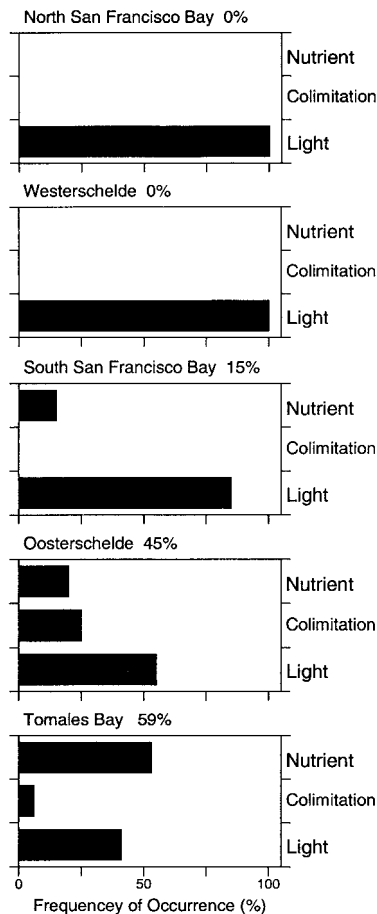


Figure 10. Frequency distributions of resource combinations that show definitive nutrient limitation (top bars), potential co-limitation by light or nutrients (middle bars), and definitive light limitation (bottom bars) for five estuaries. These distributions summarize the results of the resource-limitation index shown in Figures 5-9. Numbers above each panel give the percentage of observations showing definitive or potential nutrient limitation; these indicate the sensitivity of each estuary to change in nutrient concentration. Estuaries at the top are least sensitive to nutrient change; estuaries at the bottom are most sensitive.

these estuaries could be classified as highly sensitive to variability in nutrient loading and most susceptible to the effects of further nutrient enrichment, because they provide a light climate that does not severely constrain algal growth.

The frequency distributions of resource limitation (Figure 10) provide an index for measuring the susceptibility of individual ecosystems to one of the harmful effects of eutrophication – overproduction of phytoplankton biomass. These assessments can be done with the routine measurements of turbidity, light, and nutrient concentrations included in many mon-

itoring/research programs. As shown above, these resource assessments can be used as a basis for estuarine comparisons. They could also be used to help guide management plans for individual estuaries and their watersheds. For example, management strategies to protect water quality should give high priority to actions that would control nutrient loadings to the estuaries classified as nutrient-sensitive, such as Tomales Bay. On the other hand, management strategies might give stronger consideration to other stressors (e.g. toxic contaminants, habitat loss, exotic species) in those estuaries classified as nutrient-insensitive, such as North San Francisco Bay. The index of nutrient sensitivity described here can be used as one step in the process of prioritizing management concerns about nutrient enrichment relative to these other stressors.

Limitations to the approach

The index developed here is appealing for its simplicity, but simple models should be applied with caution and explicit recognition of their limitations. For example:

- This index measures only one response to nutrient enrichment – the stimulation of phytoplankton population *growth rate*. Stimulation of growth rate does not necessarily imply stimulation of biomass accumulation, especially in estuaries with short residence times (e.g. Balls et al., 1995; Le Pape et al., 1996) or strong grazing control of algal population development (e.g. Cloern, 1982; Herman & Scholten, 1990). The next level of complexity in the development of this index should include the effects of transports and top-down controls on phytoplankton biomass.

- This index gives no information about estuarine susceptibility to other manifestations of eutrophication, such as shifts in nutrient ratios that favor development of harmful species (Cadée & Hegeman, 1986; Radach & Hagmeier, 1990; Smetacek et al., 1991; Escaravage et al., 1996), or stimulation of macroalgal growth (Balls et al., 1995) or epiphyte growth on vascular plants (Madden & Kemp, 1996).

- Application of the index requires careful consideration of the large spatial gradients and temporal variability of light and nutrient resources that are characteristic of estuaries. The index provides meaningful information only if it is applied to data sets which represent the full spectrum of variability in the light and nutrient resources within individual estuaries. Careful application also requires consideration of the spatial

domain of concern, because the harmful effects of enrichment can be spatially disconnected from the point of nutrient delivery to the coastal zone (Rabalais et al., 1996).

With these caveats in mind, the index described here can be used as one diagnostic among the battery of tools being developed to assess and control the eutrophication threat to coastal ecosystems.

Acknowledgements

I thank Jacco Kromkamp for providing light and nutrient data for the Oosterschelde and Westerschelde estuaries, Brian Cole and Tara Schraga for their careful reviews of this manuscript, and Jens Borum for sharing his figure reproduced in Figure 1a.

References

- Alpine AE and Cloern JE (1988) Phytoplankton growth rates in a light-limited environment, San Francisco Bay. *Mar Ecol Prog Ser* 44: 167–173
- Alpine AE and Cloern JE (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnol Oceanogr* 37: 946–955
- Balls PW, Macdonald A, Pugh K and Edwards AC (1995) Long-term nutrient enrichment of an estuarine system: Ythan, Scotland (1958–1993). *Environ Pollut* 90: 311–321
- Bauerfeind E, Hickle W, Niermann U and Westernhagen HV (1990) Phytoplankton biomass and potential nutrient limitation of phytoplankton development in the southeastern North Sea in spring 1985 and 1986. *Neth J Sea Res* 25: 131–142
- Borum J (1996) Shallow waters and land/sea boundaries. In: Jørgensen BB and Richardson K (eds), *Eutrophication in Coastal Marine Ecosystems* (pp. 179–203) American Geophysical Union, Washington DC
- Boynton WR, Kemp WM and Keefe CW (1982) A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy VS (ed.), *Estuarine Comparisons* (pp. 69–90) Academic Press, New York
- Cadée GC and Hegeman J (1986) Seasonal and annual variation in *Phaeocystis pouchetii* (Haptophyceae) in the westernmost inlet of the Wadden Sea during the 1973 to 1985 period. *Neth J Sea Res* 20: 29–36
- Caffrey JM, Cole BE, Cloern JE, Rudek JR, Tyler AC and Jassby AD (1994) Studies of the San Francisco Bay, California, Estuarine Ecosystem. Pilot regional monitoring results, 1993. U.S. Geological Survey Open-File Report 94–82
- Carignan R and Planas D (1994) Recognition of nutrient and light limitation in turbid mixed layers: three approaches compared in the Paraná floodplain (Argentina). *Limnol Oceanogr* 39: 580–596
- Chapelle A, Lazare P and Ménesguen A (1994) Modelling eutrophication events in a coastal ecosystem. Sensitivity analysis. *Est Coast Shelf Sci* 39: 529–548
- Cloern JE (1982) Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar Ecol Prog Ser* 9: 191–202
- Cloern JE, Cole BE, Wong RLJ and Alpine AE (1985) Temporal dynamics of estuarine phytoplankton: a case study of San Francisco Bay. *Hydrobiologia* 129: 153–176
- Cloern JE (1987) Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Cont Shelf Res* 7: 1367–1382
- Cloern JE, Grenz G and Videgar-Lucas L (1995) An empirical model of the phytoplankton chlorophyll:carbon ratio – the conversion factor between productivity and growth rate. *Limnol Oceanogr* 40: 1313–1321
- Cloern JE (1996) Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. *Rev Geophysics* 34: 127–168
- Cole BE, Hager SW and Hollibaugh JT (1990) Hydrographic, biological, and nutrient properties of Tomales Bay, California, March 1985 to May 1986. U.S. Geological Survey Open-File Report 90–178
- Colijn F (1984) Characteristics of primary production in the Dutch Wadden Sea. *Neth Inst Sea Res Publ Ser* 10: 41–50
- DeGroot EG and de Jonge VN (1990) Effects of changes in turbidity and phosphate influx on the ecosystem of the Ems estuary as obtained by a computer simulation model. *Hydrobiologia* 195: 39–47
- de Jonge VN, Boynton W, D'Elia CF, Elmgren R and Welsh BL (1995) Responses to developments in eutrophication in four different North Atlantic estuarine systems. In: Dyer KR and Orth RJ (eds), *Changes in Fluxes in Estuaries* (pp. 179–196) Olsen and Olsen, Fredensborg, Denmark
- Dillon PJ and Rigler FH (1975) A simple method for predicting the capacity of a lake for development based on lake trophic status. *J Fish Res Board Can* 32: 1519–1531
- Escaravage V, Prins TC, Smaal AC and Peeters JCH (1996) The response of phytoplankton communities to phosphorus input reduction in mesocosm experiments. *J Exp Mar Biol Ecol* 198: 55–79
- Fisher TR, Peele ER, Ammerman JW and Harding LW Jr. (1992) Nutrient limitation of phytoplankton in Chesapeake Bay. *Mar Ecol Prog Ser* 82: 51–63
- Gowen RJ, Tett P and Jones KJ (1992) Predicting marine eutrophication: the yield of chlorophyll from nitrogen in Scottish coastal waters. *Mar Ecol Prog Ser* 85: 153–161
- Granéli E (1987) Nutrient limitation of phytoplankton biomass in a brackish water bay highly influenced by river discharge. *Estuar Coast Shelf Sci* 25: 555–565
- Hager SW (1994) Dissolved nutrient and suspended particulate matter data for the San Francisco Bay estuary, California, October 1991 through November 1993. U.S. Geological Survey Open-File Report 94–471
- Hager SW and Schemel LE (1996) Dissolved inorganic nitrogen, phosphorus and silicon in South San Francisco Bay. I. Major factors affecting distributions. In: Hollibaugh JT (ed.), *San Francisco Bay, The Ecosystem* (pp. 189–215) Pacific Division, American Association for the Advancement of Science, San Francisco
- Harding LW Jr. (1994) Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. *Mar Ecol Prog Ser* 104: 267–291
- Herman PJ and Scholten H (1990) Can suspension-feeders stabilise estuarine ecosystems? In: Barnes M and Gibson RN (eds) *Trophic Relationships in the Marine Environment* (pp. 104–116) Aberdeen University Press
- Hildebrand FG (1974) *Introduction to Numerical Analysis*. McGraw Hill, New York

- Kromkamp J and Peene J (1995) Possibility of net phytoplankton primary production in the turbid Schelde Estuary (SW Netherlands). *Mar Ecol Prog Ser* 121: 249–259
- Le Pape O, Del Amo Y, Ménesguen A, Aminot A, Quequiner B and Treguer P (1996) Resistance of a coastal ecosystem to increasing eutrophic conditions: the Bay of Brest (France), a semi-enclosed zone of Western Europe. *Cont Shelf Res* 16: 1885–1907
- Lohrenz SE, Dagg MJ and Whitledge TE (1990) Enhanced primary production at the plume/oceanic interface of the Mississippi River. *Cont Shelf Res* 10: 639–664
- Madden CJ and Kemp WM (1996) Ecosystem model of an estuarine submersed plant community: calibration and simulation of eutrophication responses. *Estuaries* 19: 457–474
- Millard ES, Myles DD, Johannsson OE and Ralph KM (1996) Seasonal phosphorus deficiency of Lake Ontario phytoplankton at two index stations: light versus phosphorus limitation of growth. *Can J Fish Aquat Sci* 53: 1112–1124
- Monbet Y (1992) Control of phytoplankton biomass in estuaries: A comparative analysis of microtidal and macrotidal estuaries. *Estuaries* 15: 563–571
- Nixon SW (1992) Quantifying the relationship between nitrogen input and the productivity of marine ecosystems. In: Takahashi M, Nakata K and Parsons TR (eds), *Proceedings of Advanced Marine Technology Conference*, Vol. 5 (pp. 57–83) Tokyo, Japan
- Nixon SW (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199–219
- Oviatt C, Doering P, Nowicki B, Reed L, Cole J and Frithsen J (1995) An ecosystem level experiment on nutrient limitation in temperate coastal marine environments. *Mar Ecol Prog Ser* 116: 171–179
- Paasche E and Erga SR (1988) Phosphorus and nitrogen limitation of phytoplankton in the inner Oslofjord (Norway). *Sarsia* 73: 229–243
- Pennock JR and Sharp JH (1994) Temporal alternation between light- and nutrient-limitation of phytoplankton production in a coastal plain estuary. *Mar Ecol Prog Ser* 111: 275–288
- Pennock JR, Sharp JH and Schroeder WS (1994) What controls the expression of estuarine eutrophication? Case studies of nutrient enrichment in the Delaware Bay and Mobile Bay estuaries, USA. In: Dyer KR and Orth RJ (eds), *Changes in Fluxes in Estuaries* (pp. 139–146) Olsen and Olsen, Fredensborg, Denmark
- Peterson DH, Schemel LE, Smith RE, Harmon DD and Hager SW (1987) The flux of particulate organic carbon in estuaries: Phytoplankton productivity and oxygen consumption. U.S. Geological Survey Water Supply Series, Selected Papers in the Hydrologic Sciences, p. 41–49
- Platt T, Sathyendranath S and Ravindran P (1990) Primary production by phytoplankton: analytic solutions for daily rates per unit of water surface. *Proc R Soc London Ser B* 241: 101–111
- Platt T, Bird DF and Sathyendranath S (1991) Critical depth and marine primary production. *Proc R Soc London Ser B* 246: 205–217
- Prins TC, Escaravage V, Smaal AC and Peeters JCH (1995) Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. *Ophelia* 41: 289–315
- Rabalais NN, Turner RE, Justić D, Dortch Q, Wiseman WJ Jr. and Sen Gupta BK (1996) Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. *Estuaries* 19: 386–407
- Radach G, Berg J and Hagmeier E (1990) Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Helgoland and at LV ELBE 1 in the German Bight. *Cont Shelf Res* 10: 305–328
- Richardson K and Heilmann JP (1995) Primary production in the Kattegat: Past and present. *Ophelia* 41: 317–328
- Riemann B, Nielsen TG, Horsted SJ, Bjørnsen PK and Pock-Stein J (1988) Regulation of phytoplankton biomass in estuarine enclosures. *Mar Ecol Prog Ser* 48: 205–215
- Rosenberg R and Loo L-O (1988) Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia* 29: 213–225
- Smetacek V, Bathmann U, Nöthig E-M and Scharek R (1991) Coastal eutrophication: causes and consequences. In: Mantoura RFC, Martin J-M and Wollast R (eds), *Ocean Margin Processes in Global Change* (pp. 251–279) John Wiley & Sons
- Visser AW and Kamp-Nielsen L (1996) The use of models in eutrophication studies. In: Jørgensen BB and Richardson K (eds.) *Eutrophication in Coastal Marine Ecosystems* (pp. 221–242) American Geophysical Union, Washington D.C.
- Vollenweider RA and Kerekes J (1980) The loading concept as basis for controlling eutrophication: philosophy and preliminary results of the OECD programme on eutrophication. *Prog Water Technol* 12: 5–38
- Wetsteyn LPMJ and Kromkamp JC (1994) Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980–1990). *Hydrobiologia* 282/283: 61–78
- Wienke SM, Cole BE and Cloern JE (1993) Plankton studies in San Francisco Bay, California. XIV. Chlorophyll distributions and hydrographic properties of San Francisco Bay, 1992. U.S. Geological Survey Open-File Report 93–423
- Wofsy S (1983) A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. *Limnol Oceanogr* 28: 1144–1155